

Genetic Diversity in the Clonal Plant *Arabis flagellosa* Miq. (Brassicaceae)

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栄養繁殖をするスズシロソウの遺伝的多様度

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(Received on January 25, 1993)

Plants of two populations of the clonal *Arabis flagellosa* were examined using gel electrophoresis techniques. Fourteen loci were detected, but only four loci were polymorphic. Populations exhibited low genetic differentiation. Gene flow estimated by indirect methods indicated a certain amount of gene flow between populations. Populations of *A. flagellosa* had slightly higher genetic variation than other *Arabis* species with low or no clonal propagation. Populations with clonal propagation may be formed by a wide range of individuals (genotypes), from uniclonal to multiclonal. The results obtained in this study indicate that *A. flagellosa* plants may be considered as an intermediate case within this range.

Breeding systems and modes of vegetative propagation are important determinants of population genetic structure in plants capable of clonal growth (Ellstrand and Roose 1987; Murawski and Hamrick 1990; Les 1991). Most clonal terrestrial plant species possess intermediate levels of genetic diversity (Ellstrand and Roose 1987) existing as multiclonal populations.

Genetic variability in populations of clonal species

is strongly influenced by the composition of the originating population and the degree of sexual recruitment (Ellstrand and Roose 1987). The extent of genetic variability in asexual populations compared to sexual ones is still in discussion. Some empirical studies showed that in the absence of mutation and sexual recruitment, genetic variability in populations of clonal species may decline over time, presumably as a result of selection and drift (e.g., Aarssen and

Turkington 1985; Hermantz et al. 1989; Maddox et al. 1989). In contrast, however, some models suggest that asexual populations are as polymorphic as sexual ones (see Ellstrand and Roose 1987). Recent reviews of genetic variation in clonal organisms, both in plants (Ellstrand and Roose 1987) and animals (Parker 1979), indicate that populations may be unique in their genetic composition. It is therefore expected that genetic differentiation may develop among clonal populations in different habitats or localities (Silander 1984; Scheiner and Teeri 1986, 1987).

Arabis flagellosa (Brassicaceae) is a rosette-forming perennial plant that occurs in a wide variety of habitats with a certain degree of disturbance. It can reproduce vegetatively by stolons with many one-leaf "ramets" integrated and may form an extensive network of stolons in a single growing season. The main individual rosettes of this species flower extensively in early April. However, it is unknown whether natural populations found in disturbed areas are the result of rapid clonal expansion of few isolated individuals or formed by extensive seeding recruitment. Previous observations on populations of this species provided contrasting results. Plants presented a low seed-set and almost no recruitment by seedlings in natural populations, indicating that clonal growth is an important mode of reproduction (Oyama unpub.). However, populations exhibited different patterns of mortality of clones and vegetative reproduction, suggesting that the contribution of both sexual and vegetative reproduction may differ between populations

Table 1. Allele frequencies for four polymorphic loci of two populations of *Arabis flagellosa*.

Population	Allele	Locus			
		Idh	Mdh-1	Mdh-2	Pgm-2
Kibune	a	0.70	0.66	1.00	0.38
	b	0.30	0.34	0.00	0.62
Kumogahata	a	0.74	0.61	0.93	0.24
	b	0.26	0.39	0.07	0.76

Table 2. Summary of allozyme variation for 13 loci in two populations of *Arabis flagellosa*. Sample sizes (N), proportion of polymorphic loci (P), number of alleles per polymorphic locus (A_p), mean number of alleles (A), and expected heterozygosity ($H_e \pm \text{s.e.}$).

Population	N	P	A_p	A	H_e
Kibune	30	0.21	2.0	1.14	0.72 ± 0.07
Kumogahata	30	0.29	2.0	1.29	0.67 ± 0.11

(Oyama unpub.).

As a part of a more comprehensive research project on comparative population biology of *Arabis* species in Japan, we investigated the genetic diversity of two populations of *A. flagellosa* in the northern area of Kyoto City.

Materials and Methods

The study sites were located along asphalt road ways in Kibune and Kumogahata towns in Kyoto. Leaves were collected regularly along transects throughout the populations. Sampling was done avoiding collection of leaves from stolons of the same individuals. Thirty samples per population were collected in plants separated at least by one meter. Electrophoretic analyses were done following the procedures indicated in Ito and Ono (1990).

Results and Discussion

The following loci were detected: Ald, G3Pdh, Idh, Mdh-1, Mdh-2, Me, 6Pgd-1, 6Pgd-2, Pgi-1, Pgi-2, Pgm-1, Pgm-2, Tpi-1 and Tpi-2. However, only Idh, Mdh-1, Mdh-2 and Pgm-2 were polymorphic with two alleles per loci (Tables 1 and 2). Two fixation index values (F) for Mdh-1 in Kumogahata and Pgm-2 for Kibune populations deviate significantly for those genotypic values expected under a Hardy-Weinberg equilibrium, indicating a deficiency in heterozygotes at Pgm-2 (Table 3). Nei's (1987) genetic diversity parameters estimated were the gene diversity in the total population (H_T) which can be

partitioned into within-populations (H_S) and among-population (D_{ST}) components. D_{ST} and H_S are used to estimate the relative magnitude of gene differentiation (G_{ST}). Plants of *A. flagellosa* exhibited low values of G_{ST} indicating a low genetic differentiation between both populations (Table 4). This is probably due to high levels of gene flow between two populations or due to a relative short time of establishment of both populations from a common source of genotypes.

Gene flow was estimated following procedures indicated in Wright (1951) and Slatkin and Barton (1989) based on values of G_{ST} . Estimates of gene flow (Nm) less than 1.0 indicate relatively little gene flow, whereas values of 1.0 or higher suggest high levels of gene flow (Slatkin and Barton 1989). Nm values for *A. flagellosa* were very high, on average $Nm=102.7$ immigrants per generation (range from 16.4 to 249.8).

The genetic identity (I) coefficient presented by Nei (1972, 1987) ranges from 0.0 to 1.0, where a

genetic similarity value of 1.0 indicates that a population pair is genetically identical. Population of *A. flagellosa* presented a I coefficient of 0.997, indicating genetic similarity.

Populations of *A. flagellosa* exhibited higher genetic diversity values than those detected in other species of *Arabis* with very low or no vegetative propagation, like *A. serrata* and *A. stelleri* var. *japonica* (Oyama et al. unpub.). Although most genotypes in clonal plant species seem to be restricted to a single population (i.e., local genotypes) (Ellstrand and Roose 1987), both populations of *A. flagellosa* share all the same genotypes. These results contrast with those obtained in a comparative study on demography between populations of *A. flagellosa*, in which individual clones differed in several growth and reproductive traits (Oyama unpub.).

Plants with clonal propagation are genetically composed by a wide range of individuals, from uniclonal (Raven and Gregory 1972; van Oostrum et al. 1985) to multiclonal plants (Ellstrand and Roose 1987). *Arabis flagellosa* constitutes an intermediate case within this range in which "widespread" genotypes still prevail in both populations due to migration or historical factors. Although one private allele was found in one of the populations, the significance of this difference is unclear.

In conclusion, *A. flagellosa* populations present (i) a certain extent of genetic variation within populations in spite of apparently dominant clonal propagation and (ii) a low genetic differentiation between populations although some demographic and life history traits differ from each other. More extensive studies are required to clarify whether this situation is merely a local case or a general situation for plants clonally propagated in disturbed habitats.

K. O. wishes to thank Prof. M. Ono of Tokyo Metropolitan University for continuous support. Thanks to Prof. K. Iwatsuki and an anonymous re-

Table 3. Fixation indices (F) for each locus and two populations of *Arabis flagellosa*, indicating deviations from Hardy-Weinberg genotypic expectations. Significant levels were calculated by pooling genotypes and comparing these frequencies with those expected under random mating. Dashed line indicates a monomorphic locus.

Population	Locus		
	Mdh-1	Mdh-2	Pgm-2
Kibune	-0.167	—	0.192*
Kumogahata	-0.194**	-0.037	-0.078

* $P<0.05$; ** $P<0.01$

Table 4. Nei's statistics of genetic diversity for three polymorphic loci in two populations of *Arabis flagellosa*.

Locus	H_T	H_S	D_{ST}	G_{ST}
Idh	0.4024	0.402	0.0004	0.001
Mdh-1	0.463	0.462	0.001	0.002
Pgm-2	0.423	0.418	0.005	0.012

viewer for their editorial assistance. K. O. was partially supported by a grant from the National University of Mexico (DGAPA, UNAM).

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要旨

スズシロソウ *Arabis flagellosa* はストロンにより栄養繁殖を頻繁に行なうハタザオ属の植物である。本種の2集団において、酵素多型をマーカーとして用い、集団の遺伝的変異性について調査を行った。9酵素、14遺伝子座について解析を行ったが、そのうち多型を示したのは4遺伝子座のみであった。この2集団について Nei の遺伝的統計量を計算した結果、集団間分化は認められなかった。2集団で多型が認められた3遺伝子座から遺伝子多様度 (H_T) を推定したところ、0.40–0.46 であり、主に種子により繁殖する他のハタザオ属の植物の種よりも大きい値を示した。